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FEMALE COLOR AND SEX RATIO IN HYBRIDS BETWEEN *PAPILIO GLAUCUS GLAUCUS* AND *P. EURYMEDON*, *P. RUTULUS*, AND *P. MULTICAUDATUS* (PAPILIONIDAE)

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ABSTRACT. Female offspring of black *Papilio glaucus glaucus* females handpaired to *P. eurymedon*, *P. rutulus*, or *P. multicaudatus* males show variable expression of the black phenotype. Hybridization with *P. rutulus* yielded black, yellow, and intermediate females, in agreement with previous observations. Hybridization with *P. multicaudatus* also yielded black and intermediate females, which has not been reported previously. Hybridization with *P. eurymedon* yielded only one yellow female. Suppression of the black phenotype in interspecies hybrids is not complete and may not have a simple genetic basis.

The sex ratio among progeny of these hybridizations was skewed drastically towards males, with most females dying prior to adult eclosion. This "Haldane effect" appears to be much less severe among progeny of *P. glaucus glaucus* males paired to *P. eurymedon* or *P. rutulus* females than in the case of reciprocal pairings using *P. g. glaucus* females.

Additional key words: Haldane effect, mimetic coloration, suppressor genes, enabler genes, pupal diapause.

Papilio glaucus glaucus (Papilionidae) females show a striking color dimorphism that has attracted considerable study for over 100 years (Edwards 1884, Clarke & Sheppard 1959, 1962, Brower 1958, Brower 1959a, 1959b, Brower & Brower 1962, Scriber et al. 1987, Lederhouse & Scriber 1987). Female *P. g. glaucus* may have a yellow ground color and resemble the monomorphic males, or they may have a dark or black ground color and act as Batesian mimics of *Battus philenor* (Brower 1958).

Papilio g. glaucus appears to be unique among taxa within the *Papilio glaucus* species group in exhibiting this dimorphism. Only monomorphic females occur in *P. glaucus canadensis*, *P. rutulus*, *P. eurymedon*, *P. multicaudatus*, and *P. alexiares alexiares*. Only black females are known in *P. alexiares garcia* (Beutelspacher & Howe 1984). Valuable insight into the evolution of mimicry in *P. g. glaucus* can be obtained through comparative study of the genetic basis for female color in these closely related species and subspecies.

Female color in *P. g. glaucus* is almost always maternally inherited, implying that it is determined primarily by a Y-linked gene (Clarke & Sheppard 1959, 1962, Clarke & Clarke 1983). Exceptions to the usual rule of maternal inheritance (cases of black females producing yellow daughters and the reverse) have been noted repeatedly, however (Edwards 1884, Clarke & Sheppard 1959, 1962, Scriber & Evans 1986, Scriber et al. 1987). Chromosome abnormalities have been invoked as explanations for some of these cases (Clarke & Sheppard 1959, Clarke & Clarke 1983, Scriber & Evans 1987, West & Clarke 1987).

Cases of non-maternal inheritance may also result from effects of autosomal or X-linked "suppressor" alleles that inhibit the production or deposition of black ground color (Clarke & Willig 1977, Clarke & Clarke 1983, Scriber et al. 1987, West & Clarke 1987, Hagen & Scriber 1989). An X-linked suppressor of this type has been identified and mapped in *P. g. canadensis* (Hagen & Scriber 1989). Presence of the *canadensis* suppressor allele is probably responsible for reported cases of non-maternal inheritance involving females collected near the *P. g. glaucus/P. g. canadensis* hybrid zone (Scriber et al. 1987, Scriber 1988).

In the case of *P. g. canadensis,* laboratory hybridizations with *P. g. glaucus* have revealed that the absence of black females is due both to lack of the black-determining Y-linked allele and to high frequency of the X-linked suppressor allele in natural populations (J. M. Scriber, R. Hagen & R. C. Lederhouse, unpublished). Do homologous suppressors occur in other taxa also lacking a black female form?

Interspecies hybrids within the *glaucus* species group may be obtained through hand-pairing (Clarke & Sheppard 1955, 1957, West & Clarke 1987, Scriber et al. 1988, 1991). Based on such crosses, West and Clarke (1987) presented evidence for suppressors in *P. eurymedon, P. rutulus,* and *P. multicaudatus.* Here we report results of additional laboratory hybridizations between *P. g. glaucus* and *P. eurymedon, P. rutulus,* and *P. multicaudatus.* Results of hybridization with *P. alexiares garcia* have been presented elsewhere (Scriber et al. 1988).

Reduced viability of hybrid females, the heterogametic sex, may result from genetic differentiation after speciation (the "Haldane effect": Haldane 1922, Ae 1979, Oliver 1979, Coyne & Orr 1989a). Recent studies have implicated sex chromosome interactions as primary factors in sex-biased hybrid viability and fertility (Coyne 1985, Coyne & Orr 1989b). Imperfect integration of the genome of hybrid Lepidoptera can result in a syndrome of developmental and diapause abnormalities, possibly from hormonal imbalances between regulatory and secretory positions of sex-linked co-adapted gene complexes (Oliver 1983). Prolonged post-diapause development of pupae may result in delays of adult females, and diapause may extend for one or more years (Oliver 1983, Scriber et al. 1987). More extreme cases may result in death of female hybrids at the egg, larval, or pupal stage, and therefore skewed sex-ratios may serve as indicators of the negative effects of the X- and Y-chromosome interactions. Sex ratios for interspecific crosses within the *glaucus* species group are presented here.

METHODS

Male and female *P. rutulus* and *P. eurymedon* were collected from Orange, Placer, Solano, Sacramento, and Mono counties, California and the Blue Mountains (Columbia County) of Washington during 1982–90 and mailed in envelopes or carried on ice to our laboratory. *Papilio multicaudatus* were collected from Placer and Solano counties in California and Columbia County, Washington and also from Nuevo Leon, Mexico.

Male *P. rutulus, P. eurymedon,* and *P. multicaudatus* were hand-paired to lab-reared virgin *P. glaucus* females. Field collected and laboratory-mated females were set up in plastic oviposition boxes (10 cm × 20 cm × 27 cm) with a sprig of foodplant under saturated humidity. The boxes were placed 0.7–1.0 m from continuously lighted 100 watt incandescent bulbs. From 1987–90 a repeating 4:4 h photo: scotophase was used. Females were fed a mixture of 1 part honey to 4 parts water at least once daily. Most females were allowed to oviposit until death. Eggs were collected and counted at 2-day intervals. Larvae were removed as they eclosed, and the remaining eggs were monitored for 10 days after the first larva hatched. First instar (neonate) larvae were gently placed on fresh leaves of various host plants. Leaf moisture was maintained using Aquapics® and fresh leaves were provided three times a week throughout larval development. Pupae were held at room temperature (23°C) for a minimum of three months after pupation. Those that had not emerged were then refrigerated six months at 5–7°C and then held at room temperature the following summer. This procedure was repeated for those apparently alive, healthy pupae that did not emerge by the end of the second summer. Some progeny of the field-collected females were used in the subsequent matings. Hybrid crosses are given with the female parent listed first.

RESULTS

Hybridization with *Papilio eurymedon*

A total of 25 pairings of *P. g. glaucus* females and *P. eurymedon* males was successful as judged by production of offspring reaching at least the pupal stage (Table 1). Only one female eclosed successfully from these broods whereas 223 males eclosed. The number of dead or developmentally delayed pupae (250) was not greatly different from the total number of males eclosing, suggesting that the majority may have been females (sex of pupae was not determined for this portion of our study). Extremely low viability of female hybrids was independent of maternal color phenotype. Black *P. g. glaucus* females were

TABLE 1. Hybrids between *Papilio glaucus* and *P. eurymedon*.

			Offspring		
Brood no.	Mother (source)	Father (source)	Males	Females	Dead pupae
1083	black *Pgg* (OH)	*eurymedon* (CA)	13	0	5
1170	black *Pgg* (OH)	*eurymedon* (CA)	1	0	3
1196	black *Pgg* (WI)	*eurymedon* (CA)	6	0	9
2309	black *Pgg* (WVA)	*eurymedon* (CA)	0	0	1
2311	black *Pgg* (IL)	*eurymedon* (CA)	11	0	11
2312	black *Pgg* (IL)	*eurymedon* (CA)	1	0	4
2313	black *Pgg* (IL)	*eurymedon* (CA)	21	0	27
2314	black *Pgg* (WVA)	*eurymedon* (CA)	1	0	0
2315	black *Pgg* (WVA)	*eurymedon* (CA)	6	0	9
2321	black *Pgg* (WVA)	*eurymedon* (CA)	24	0	21
2322	black *Pgg* (WVA)	*eurymedon* (CA)	0	0	4
2327	black *Pgg* (IL)	*eurymedon* (CA)	14	1*	29
2328	black *Pgg* (IL)	*eurymedon* (CA)	33	0	41
2518	black *Pgg* (GA)	*eurymedon* (CA)	4	0	9
2547	black *Pgg* (WI)	*eurymedon* (WA)	1	0	1
2671	black *Pgg* (WI)	*eurymedon* (CA)	16	0	16
	Subtotal		(148)	(1)	(190)
544	yellow *Pgg* (PA)	*eurymedon* (CA)	22	0	14
1084	yellow *Pgg* (OH)	*eurymedon* (CA)	3	0	5
1117	yellow *Pgg* (OH)	*eurymedon* (CA)	2	0	0
1119	yellow *Pgg* (OH)	*eurymedon* (CA)	21	0	23
1168	yellow *Pgg* (FL)	*eurymedon* (CA)	5	0	3
1187	yellow *Pgg* (FL)	*eurymedon* (CA)	1	0	0
1198	yellow *Pgg* (FL)	*eurymedon* (CA)	0	0	1
2269	yellow *Pgg* (WVA)	*eurymedon* (CA)	15	0	11
2318	yellow *Pgg* (WVA)	*eurymedon* (CA)	6	0	3
	Subtotal		(75)	(0)	(60)
4465	*eurymedon* (WA)	*Pgg* (FL)	6	1*	0

Pgg = *Papilio glaucus glaucus*, * = yellow.

used in 16 of the pairings and yellow females in the remaining nine; the only daughter produced was from a black mother (brood 2327).

Female viability appears to be higher in the reciprocal cross (*P. eurymedon* female × *P. g. glaucus* male). Few crosses in this direction were attempted in our study and only one was successful (Table 1: brood 4465). However, one of two successful crosses in the same direction reported by West and Clarke (1987) produced 13 females and 13 males; the other produced two males only. The overall sex ratio from these three crosses was 1.5 male: 1.0 female (n = 35 offspring).

The color of the single hybrid (*P. g. glaucus* × *P. eurymedon*) female was yellow, which could indicate that her phenotype resulted from a suppressor contributed by her father. Additional evidence of a *P. eurymedon* suppressor is provided by the yellow daughters from 2 back-

TABLE 2. Backcrosses involving *P. eurymedon*.[1]

Brood no.	Mother (source)	Father (source)	Offspring Males	Offspring Females	Offspring Dead pupae
1278	black *Pgg* (TX)	F_1 (yellow *Pgg* × *Pe*)	2	1*	4
1544	black *Pgg* (TX)	F_1 (black *Pgg* × *Pe*)	3	5*	3

[1] The *P. g. glaucus* female numbers for the g × e hybrid males are 544 and 1083, respectively, for pairings 1278 and 1544.

Pgg = *Papilio glaucus glaucus*, *Pe* = *Papilio eurymedon*, * = yellow.

crosses of hybrid (*P. g. glaucus* × *P. eurymedon*) males to black *P. g. glaucus* females (Table 2). Too few offspring (6 females) were produced to determine whether yellow and black phenotypes depart significantly from the 1:1 ratio expected of a single suppressor allele contributed from the *P. eurymedon* grandparent.

The combined sex ratio among the backcross progeny (0.83 male: 1.0 female, n = 11) was similar to the combined ratio from three similar backcross families obtained by West and Clarke (1987) (1.33:1, n = 21) and neither differed significantly from a 1:1 ratio (χ^2, both P's > 0.50). Fertility of the hybrid males did not appear to be greatly reduced relative to that of other laboratory-reared males (Lederhouse et al. 1990).

Hybridization with *Papilio rutulus*

There were 26 successful pairings of *P. g. glaucus* females with *P. rutulus* males using 13 black and 13 yellow females (Table 3). As in the case of pairings with *P. eurymedon* males, most of the progeny that eclosed were male: 362 males versus 12 females (28:1 ratio). Also similar to crosses with *P. eurymedon*, a large number of pupae (407) failed to develop. Live pupae of 1987 crosses (brood #4562, 4564, and 4664) that had not emerged by August 1988 were sexed. Only 2 of the 34 pupae were male and all died subsequently without emerging. No effect of maternal color on sex ratio was apparent (Table 3). West and Clarke (1987) reported a total of 19 males and two females from two crosses of this type; two additional females were obtained by ecdysone injection of pupae (Clarke & Willig 1977).

Far fewer reciprocal crosses (*P. rutulus* female × *P. g. glaucus* male) were attempted, but the one that was successful (#4447) yielded an equal number of males and females. A similar, nearly equal, ratio of sexes (10 males, 8 females) was obtained by Clarke and Sheppard (1955) in an earlier cross of this type. Fertility of hybrid males, backcrossed to *P. g. glaucus* females did not appear to be substantially impaired (Table 4; also West & Clarke 1987). The sex ratio among backcross

TABLE 3. Hybrids between *Papilio glaucus* and *P. rutulus*.

			Offspring		
Brood no.	Mother (source)	Father (source)	Males	Females	Dead pupae
1115	black *Pgg* (WI)	*rutulus* (CA)	0	0	2
1152	black *Pgg* (FL)	*rutulus* (CA)	0	0	1
1153	black *Pgg* (FL)	*rutulus* (CA)	1	1+	0
1155	black *Pgg* (WI)	*rutulus* (CA)	15	2+	18
1156	black *Pgg* (OH)	*rutulus* (CA)	16	0	16
1181	black *Pgg* (FL)	*rutulus* (CA)	3	0	4
1183	black *Pgg* (OH)	*rutulus* (CA)	5	1*	7
2517	black *Pgg* (GA)	*rutulus* (WA)	43	1*	33
2553	black *Pgg* (GA)	*rutulus* (WA)	2	0	1
2830	black *Pgg* (WVA)	*rutulus* (CA)	40	0	15
4562	black *Pgg* (FL)	*rutulus* (CA)	47	2*	41
4564	black *Pgg* (FL)	*rutulus* (CA)	2	0	1
4664	black *Pgg* (OH)	*rutulus* (CA)	24	0	12
	Subtotal		(198)	(7)	(151)
2	yellow *Pgg* (PA)	*rutulus* (CA)	18	0	30
277	yellow *Pgg* (PA)	*rutulus* (CA)	15	2*	25
433	yellow *Pgg* (PA)	*rutulus* (CA)	12	0	17
546	yellow *Pgg* (WI)	*rutulus* (CA)	6	0	4
547	yellow *Pgg* (PA)	*rutulus* (WA)	30	1*	68
548	yellow *Pgg* (WI)	*rutulus* (WA)	9	0	11
1179	yellow *Pgg* (WI)	*rutulus* (CA)	33	0	23
334	yellow *Pgg* (FL)	*rutulus* (CA)	7	0	19
335	yellow *Pgg* (FL)	*rutulus* (CA)	2	0	8
336	yellow *Pgg* (FL)	*rutulus* (CA)	6	0	29
343	yellow *Pgg* (FL)	*rutulus* (CA)	0	0	2
1178	yellow *Pgg* (FL)	*rutulus* (CA)	9	2*	2
1180	yellow *Pgg* (FL)	*rutulus* (CA)	17	0	18
	Subtotal		(164)	(5)	(256)
4465	*rutulus* (CA)	*Pgg* (FL)	5	5	2

Pgg = *Papilio glaucus glaucus*, * = yellow, + = black.

progeny was 2.4 male: 1.0 female (n = 150 offspring), similar to the ratio 2:1 (n = 71) reported by West and Clarke (1987).

Five pairings with black *P. g. glaucus* females produced a total of 3 black and 4 yellow hybrid (F1) daughters (Table 3, Fig. 1). Mixed phenotypes (two yellow, two intermediate) were also reported by West and Clarke (1987) from crosses of this type. (Hybrid intermediates are figured in Clarke & Willig [1977] and Clarke & Clarke [1983].) Three successful backcrosses of F1 males to black *P. g. glaucus* females also produced a range of color phenotypes among daughters (Table 4). The majority of backcross females were intermediate in color, with varying proportions of black and yellow scales intermixed (Fig. 1c–f). Four backcrosses of this type reported by West and Clarke (1987) also yielded

TABLE 4. Backcrosses involving *Papilio rutulus*.[1]

			Offspring					
				Females				
Brood no.	Mother (source)	Father (source)	Males	Black	Mostly dark	Mostly yellow	Yellow	Dead pupae
630	black *Pgg* (WI/SC)	F_1 (yellow *Pgg* × *Pr*) (CA)	32	3	5	4	1	15
1875	black *Pgg* (WI)	F_1 (black *Pgg* × *Pr*) (CA)	23	5	7	3	1	39
1876	black *Pgg* (WI)	F_1 (black *Pgg* × *Pr*) (CA)	51	2	12	1	8	27

Pgg = *Papilio glaucus glaucus*, *Pr* = *Papilio rutulus*.

[1] The *P. g. glaucus* female numbers for the g × r hybrid males are 433, 1155, and 1183 respectively for pairings 630, 1875, and 1876.

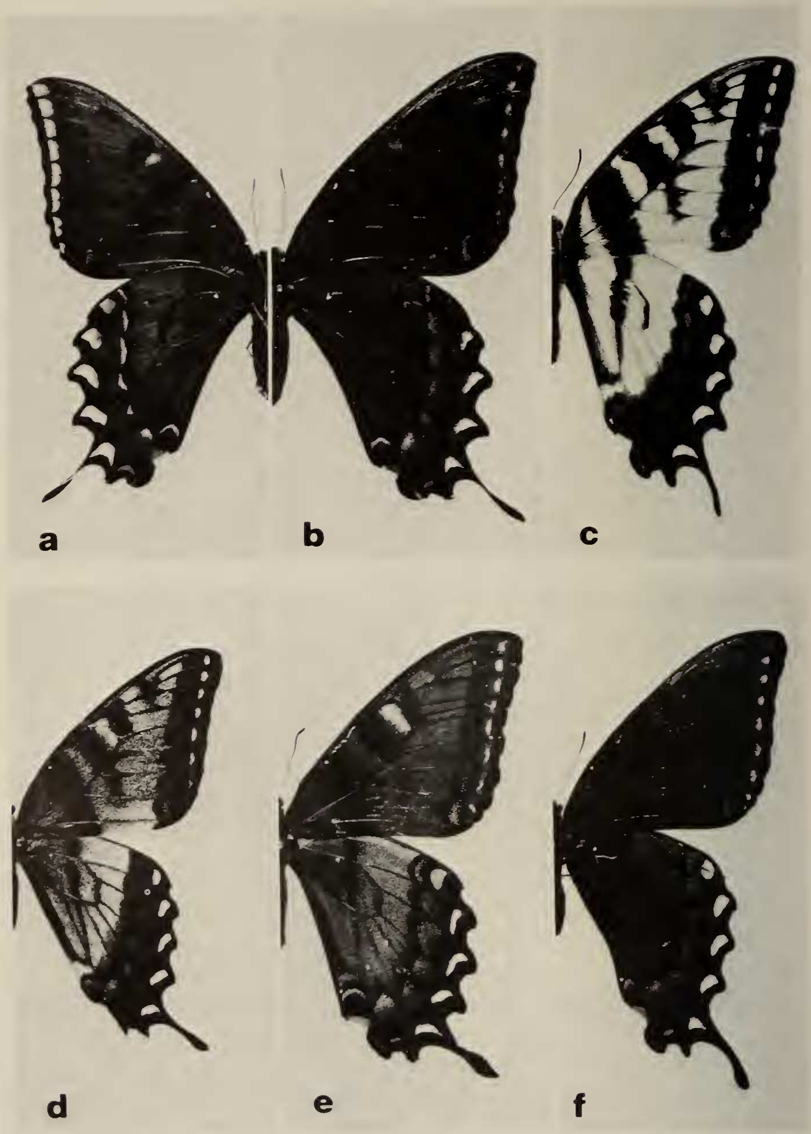

FIG. 1. Ventral (a) and dorsal (b) views of a black female hybrid from a black female *P. g. glaucus* × male *P. rutulus* (brood #1153). Backcross offspring exhibiting four female color forms (yellow [c], "intermediate" mostly yellow [d], "intermediate" mostly black [e], and black [f]). These 4 females are from a single backcross (brood #1876) between a dark *P. g. glaucus* female and a hybrid male (from a black female *glaucus* × male *rutulus*).

TABLE 5. Hybrids between *Papilio glaucus* and *P. multicaudatus*.

			Offspring				
Brood no.	Mother (source)	Father (source)	Males	Black females	Inter-mediate females	Yellow females	Dead pupae
2265	black *Pgg* (OH)	*multicaudatus* (CA)	10	2	3	0	10
3619	black *Pgg* (GA)	*multicaudatus* (WA)	4	1	0	0	0
3660	black *Pgg* (OH)	*multicaudatus* (Mex)	1	0	0	0	3
4473	black *Pgg* (OH)	*multicaudatus* (Mex)	2	0	0	0	4
4475	black *Pgg* (IN)	*multicaudatus* (Mex)	1	0	0	0	1
4498	black *Pgg* (FL)	*multicaudatus* (Mex)	10	0	0	0	9
4512	black *Pgg* (IN)	*multicaudatus* (Mex)	0	0	0	0	3
4516	black *Pgg* (OH)	*multicaudatus* (Mex)	2	0	0	0	1
	Subtotal		(30)	(3)	(3)	(0)	(31)

Pgg = *Papilio glaucus glaucus*.

a mixture of phenotypes (16 black; 5 intermediate; 3 yellow). Differences in the proportions of black and intermediate females between studies may reflect differences in criteria used for phenotype classification.

Hybridization with *Papilio multicaudatus*

We obtained eight successful pairings of black *P. g. glaucus* females with *P. multicaudatus* males (Table 5). No pairings with yellow females were successful and we did not have sufficient *P. multicaudatus* females to attempt reciprocal pairings using *P. g. glaucus* males. Two pairings yielded a total of six female offspring, for an overall sex ratio of 5:1 male : female (n = 36 offspring). Pupae from broods #2265, 3660, 4473, 4498, and 4516 that were alive, but had not eclosed after one year were sexed. All ten were female and all died without eclosing. West and Clarke (1987) report only male offspring in crosses in this type.

The hybrid females consisted of three black and three intermediate individuals (Fig. 2). The intermediate phenotype may indicate partial suppression of the black color in these hybrids. West and Clarke (1987) postulate the occurrence of a *P. multicaudatus* suppressor on the basis of 2 yellow daughters obtained from a backcross of a hybrid male to a black *P. g. glaucus* female.

Miscellaneous Interspecific Crosses

Five pairings of *P. rutulus* females with *P. eurymedon* males and five of the reciprocal pairings were successful (Table 6, Fig. 3). Despite overall low numbers of emerging adults, hybrid females were obtained from both types. The one successful hybridization between a *P. eurymedon* female and a *P. multicaudatus* male also yielded both male

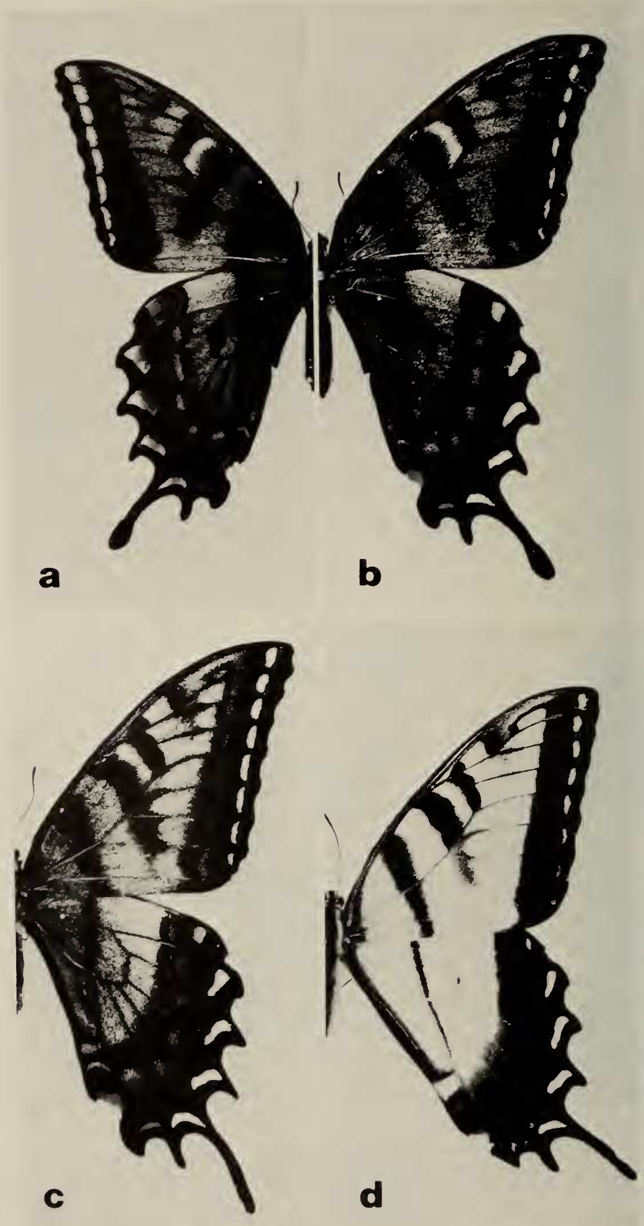

FIG. 2. Hybrid offspring (brood #2265) of a black female of *P. g. glaucus* × male *P. multicaudatus*. Ventral (a) and dorsal (b) views of a black female with some yellow scaling and the dorsal view (c) of an intermediate female are shown. The lower right (d) is a sibling hybrid male.

TABLE 6. Hybrids and backcrosses between *P. rutulus*, *P. eurymedon*, and *P. multicaudatus*.

			Offspring		
Brood no.	Mother (source)	Father (source)	Males	Females	Dead pupae
4539	*rutulus* (CA)	*eurymedon* (OR)	0	1	0
5653	*rutulus* (OR)	*eurymedon* (CA)	1	0	0
88008	*rutulus* (CA)	*eurymedon* (CA)	9	3	6
89028*	*rutulus* (CA)	*eurymedon* (CA)	22	9	0
7807*	*rutulus* (CA)	*eurymedon* (CA)	9	9	0
	Subtotal		(41)	(22)	(6)
1112	*eurymedon* (CA)	*rutulus* (CA)	3	1	3
3468	*eurymedon* (CA)	*rutulus* (WA)	1	0	15
3471	*eurymedon* (CA)	*rutulus* (WA)	0	2	27
3472	*eurymedon* (CA)	*rutulus* (WA)	1	0	7
89009*	*eurymedon* (CA)	*rutulus* (WA)	3	0	0
	Subtotal		(8)	(3)	(52)
88009	(*Pr* × *Pe*)	*rutulus* (CA)	9	9	2
7805	*rutulus* (CA)	*multicaudatus* (CA)	0	1	0
7806*	*rutulus* (CA)	*multicaudatus* (CA)	4	4	0
7819*	*rutulus* (CA)	*multicaudatus* (CA)	5	5	0
	Subtotal		(9)	(10)	(0)
4515	*eurymedon* (CA)	*multicaudatus* (Mex)	4	3	7

Pr = *Papilio rutulus*, *Pe* = *Papilio eurymedon*.
* Numbers reported are for sexed pupae.

and female offspring (Table 6). Three pairings of *P. rutulus* females with *P. multicaudatus* males produced a nearly equal sex ratio in pupae although more female pupae diapaused. All of the hybrid females in these crosses were yellow (Fig. 3).

DISCUSSION

In general, results from interspecific hybridizations in our laboratory agree with those summarized by West and Clarke (1987), with respect to relative viability of sexes and inheritance of color in female progeny. In both studies, however, relatively small sample sizes limit our ability to infer the genetics underlying these observations. Nonetheless, some generalizations can be suggested on the basis of present knowledge.

Suppressors of Black Female Color

Our results provide additional evidence to support West and Clarke's claim that suppressors of the black female phenotype occur in *P. eurymedon*, *P. rutulus*, and *P. multicaudatus*.

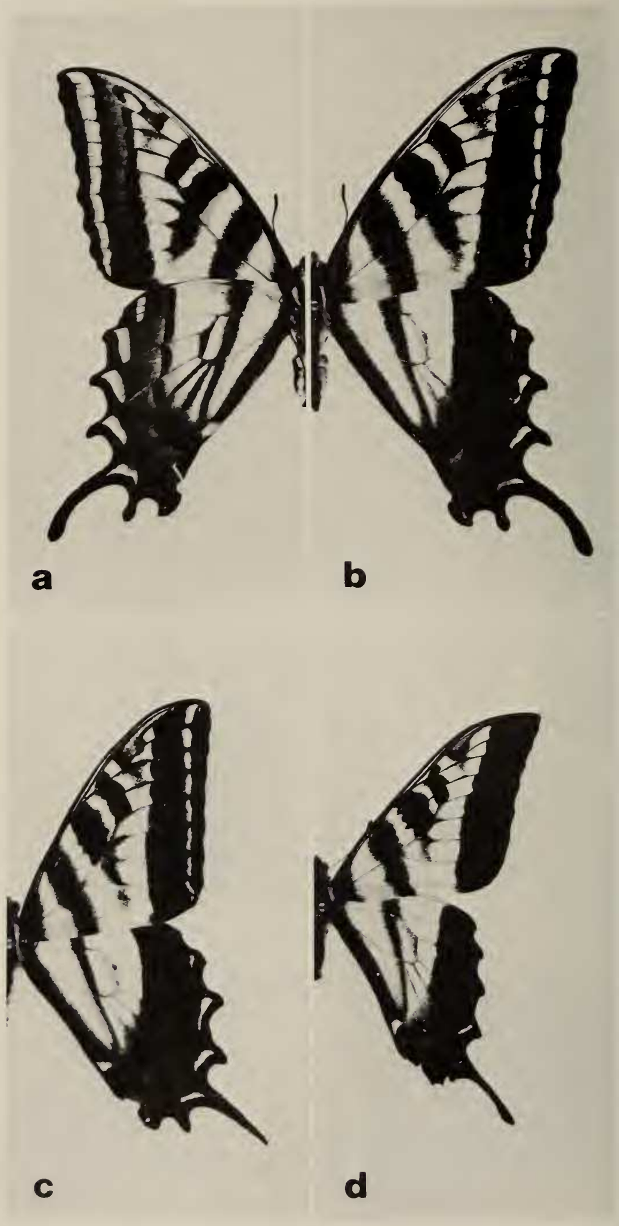

FIG. 3. Hybrid offspring of a female *P. eurymedon* × *P. multicaudatus* (brood #4515). Ventral (a) and dorsal (b) views of a female and the dorsal (c) view of a male are shown. The dorsal view (d) of a male offspring of a female *P. rutulus* × a male *P. eurymedon* (brood #88008) is also shown.

West and Clarke (1987) argue that suppression in *P. eurymedon* is due to an autosomal gene, in contrast to the X-linked suppressor of *P. glaucus canadensis* (Hagen & Scriber 1989). However, their argument is based on the occurrence of one yellow female in a backcross family, and should be accepted with caution. Unfortunately, our data provide little additional evidence of the mode of inheritance for any of the suppressors.

The *P. rutulus* and *P. multicaudatus* suppressors appear to be less effective than that of *P. eurymedon*, based on presence of intermediate and black females among hybrid or backcross progeny. As noted by West and Clarke (1987) and others (Scriber & Evans 1986, Hagen & Scriber 1989, J. M. Scriber, R. Hagen, and R. C. Lederhouse unpublished), inheritance of female color in *P. g. glaucus* crosses does not always follow simple Mendelian patterns. Further *P. g. glaucus* × *P. eurymedon* crosses and backcrosses are needed to determine whether there is consistent autosomal inheritance of suppression, and whether the "*eurymedon* suppressor" is truly different from those of other species.

From an evolutionary perspective, the presence of suppressors in *P. eurymedon, P. rutulus, P. multicaudatus,* and *P. g. canadensis* is puzzling if their only function is to prevent expression of the black female phenotype. All four taxa lack the Y-linked allele that is required to produce black females in the first place. Moreover, ranges of the three western species overlap considerably with that of *Battus philenor* (Ferris & Brown 1981, Scott 1986), so there is a potential selective advantage favoring black females if they were to appear in these species. One plausible explanation is that suppression is a pleiotropic effect of genes that play other, more significant roles in these butterflies. Their effect in hybrids may be an artifact of the disruption of both parental genomes.

Another possibility is that "suppressor" loci are actually "enabler" genes in *P. g. glaucus* and *P. alexiares garcia*. Suppression of the black phenotype may be a consequence of the absence of a required factor, rather than the presence of a specific inhibitor. If true, this would account for the simultaneous absence of the Y-linked allele and presence of suppression in *P. glaucus* group taxa lacking black females (i.e., *P. rutulus, eurymedon, multicaudatus,* and *P. g. canadensis*). The origin of the black female phenotype may have required evolution at two or more loci: at a Y-linked "black pigment" locus, and at X-linked or autosomal "enabler/suppressor" loci. The variable expression of female color in hybrids may represent a preadaptation for the black phenotype that was present in the ancestor of *P. g. glaucus* before the evolution of the Y-linked allele.

Sex Ratios and Viability of Interspecies Crosses

Analysis of inheritance patterns for female color in this study was limited primarily by low viability of female progeny in crosses of the type best able to demonstrate suppression: *P. g. glaucus* female × *P. eurymedon, rutulus,* or *multicaudatus* male. These females will have *P. g. glaucus* cytoplasm and Y-chromosome but have only a *eurymedon, rutulus,* or *multicaudatus* X-chromosome. Since low female viability occurred among daughters of both yellow and black *P. g. glaucus,* the Y-linked color gene appears not to be directly responsible.

Differential mortality of hybrid females appears to occur in the pupal stage. The numbers of dead pupae are roughly equal to the number of males that emerged in each family (Tables 1, 3, 5). When the sex of pupae was determined, the majority of those pupae that failed to develop were female. If these subsamples were representative of all dead hybrid pupae, family sex ratios would much more closely approximate the 1:1 ratio shown by intraspecific crosses.

In *P. g. canadensis,* the X-linked suppressor is closely linked to a locus responsible for regulation of pupal diapause (Hagen & Scriber 1989). The *canadensis* allele at this diapause locus causes individuals carrying it to enter an "obligate" pupal diapause, irrespective of photoperiod, temperature, or other cues (Rockey et al. 1987a, 1987b, Hagen & Scriber 1989). The *canadensis* allele appears to be recessive to the *glaucus* allele which permits environmental avoidance of diapause. Therefore, among hybrid *P. g. glaucus* × *P. g. canadensis* progeny reared under diapause-averting conditions, individuals entering pupal diapause were nearly all females.

Female mortality in interspecies crosses may involve homologous sex-linked regulatory loci that prevent triggering of pupal development in hybrids. Ecdysone injected into hybrid pupae has proven effective for stimulating ecolsion of hybrids and may provide a means for overcoming this block artificially (Clarke & Willig 1977, Hagen & Scriber 1989).

West and Clarke (1987) summarize the genetic basis underlying the human "fragile-X" syndrome as an example of the potential for subtle genotype-by-environment interactions affecting phenotype at the chromosomal level. Gilbert et al. (1987) described multiple pathways for genetic control of coloration in *Heliconius* species. It remains to be seen whether a single genetic mechanism underlies the diverse patterns of inheritance of color phenotype in the *Papilio glaucus* group, and whether it is connected directly with evolution of barriers to reproduction between species.

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